SOME WATER RELATIONS OF THREE WESTERN GRASSES. I. THE TRANSPIRATION RATIO [1]

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In regions of low rainfall, such as in the western grasslands of the United States, plants useful for soil conservation must not only be adapted to binding soil, but they must also be physiologically suited to withstand periods of drought without excessive injury. It is desirable that they should be economical in their use of the limited supply of moisture. In this paper the transpiration ratios of three western grasses commonly used for soil-conservation purposes are considered.

Agropyron Smithii Rydb., *Bromus marginatus* Nees., and *Agropyron ciliare* (Trin.) Franch. were the grasses used in this study. The first two of these are native to the western part of the United States and have been shown to be good soil-conserving plants in at least certain restricted areas. They produce good seed crops with a high percentage of fertility, and their forage values are satisfactory (Sampson, 1924). *Agropyron ciliare* is an Asiatic species which has been introduced into the United States and has been grown at several experiment stations. All three species are perennials.

The term "transpiration ratio" is used in this paper to indicate the ratio between the amount of water transpired by the plant during its growth and the weight of dry matter produced. This term is synonymous with the "water requirement" of Briggs and Shantz (1913b).

Briggs and Shantz and co-workers (Briggs and Shantz, 1914, 1917; Shantz and Piemeisel, 1927; Dillman, 1931) made extensive studies of the transpiration ratios of plants adapted to the dry regions of the United States. Several grasses that occur commonly in the Great Plains were included in their investigations. Their work was done at Akron, Colorado, Newell, South Dakota, and Mandan, North Dakota. *Agropyron Smithii* was found to be one of the most extravagant plants, requiring more water to produce a gram of dry weight than alfalfa and considerably more than the grain crops. *Agropyron cristatum* and *Bromus inermis* were somewhat more efficient. The short grasses (*Bouteloua gracilis* and *Buchloë dactyloides*) were very economical in their use of water. *Sorghum vulgare* var. *sudanense* had a low transpiration ratio. Several other investigators have found this grass to be particularly economical with respect to water utilization (Miller, 1916; Tulaikov, 1926; Ballard, 1933).

Sampson and Weyl (1918) and Sampson (1919) are the only other investigators who have reported the transpiration ratio for any of the western grasses. They obtained the value 1,339 for *Bromus marginatus* on eroded soil, and 1,110 on soil that had not been eroded. Sampson also reports the transpiration ratio for this grass as 803, 516, and 756 in oak-brush, aspen-fir, and spruce-fir associations, respectively.

In each of these investigations the transpiration ratios of the grasses studied were found, with a few exceptions, to be materially higher than those for other types of plants characteristic of the western grasslands. However, Sampson (1919) pointed out that the root growth of grasses forms a much higher percentage of the total plant growth than does the root growth of crop plants, such as wheat and peas. Consequently, the common practice of using only the dry weight of tops produced as a basis for the transpiration ratios of such plants gives misleading results, unless forage production alone is being considered.

Methods.—*Experiments of 1937*.—In these experiments plants were grown in sealed impermeable pots which were weighed frequently to determine the quantity of transpiration. At the time of each weighing the transpired water was replaced, and at the end of the growing season the total loss of water was computed. The transpiration ratio was obtained by dividing the total transpiration by the dry weight produced.

The potometers used were made of heavily galvanized iron (fig. 1). They measured 35 cm. in diameter and 50 cm. in height and had a capacity of about 35 kg. of oven-dry soil. The soil used was a fertile sandy loam which had been prepared for greenhouse purposes. The surface of the soil in each can was covered with a disk of heavy cardboard which had been thoroughly impregnated and coated with paraffin. The melting point of this paraffin was 70°C. A preliminary experiment demonstrated that this type of cover, when sealed to the can with Plasteline, did not allow measurable quantities of water to evaporate from the soil. A disk of painted cardboard placed over the cover prevented the melting of the paraffin on excessively warm days.

Water was introduced into the pots through a large-diameter glass tube which was situated near one edge of the pot. One end of this tube passed through the paraffined cover, and the other end terminated in the soil with a U-shaped extension, the two arms of which followed the contour of the pot for several inches. The ends of the U-tube were enclosed in galvanized-iron wire gauze wrapped in absorbent paper which served as a wick to disperse the water rapidly. The U-tubes with the wicks were buried in a one-half inch layer of sand which further aided in dispersing the water rapidly and evenly

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throughout the pot. Each of the pots was equipped with two of these watering systems placed at distances of one-third and two-thirds of the total depth of the pot. Thus the water was introduced at two levels and at four different points (fig. 1). A vial was kept over the inlet tube except at times when water was being introduced. This system of watering was found to be very satisfactory, and it is believed that the moisture was distributed evenly through the soil, since the roots penetrated every portion of the soil, and there was no tendency for them to mass at the wicks.

All the grasses used in these experiments were grown from seed collected in northern Colorado. A single small seedling was transplanted into each potometer, six potometers being used for each species. The use of seedlings at the beginning of the experiment introduces a small error into the growth factor of the transpiration ratio. In order to correct for this, five seedlings for each species were dried at the time of transplanting and the average dry weight determined. This was subtracted from the final dry weight produced in each potometer during the experimental period. Uniform seedlings were chosen for the transplanting and for the initial drying.

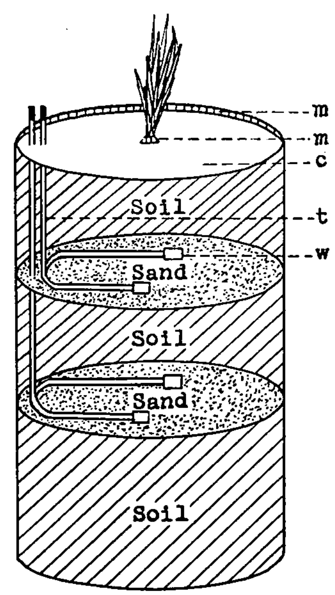
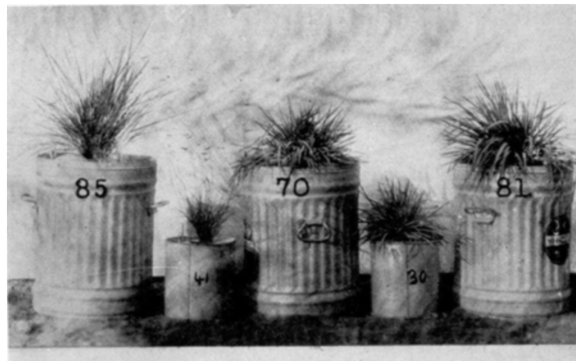


Fig. 1. Potometer with watering device. m, modeling clay; c, paraffined cover; w, wire wick; t, glass tube.

The potometers were left in the greenhouse for two weeks following planting, after which they were removed to the field site of the experiments. This site was located in an exposed portion of the Botanical Gardens of the University of Michigan. It consisted of a trench 35 feet in length and 4 feet in width, the long axis extending from east to west (fig. 3). The walls were lined with boards, and a wooden platform covered the floor. The trench had sufficient depth to permit the tops of the cans to be level with



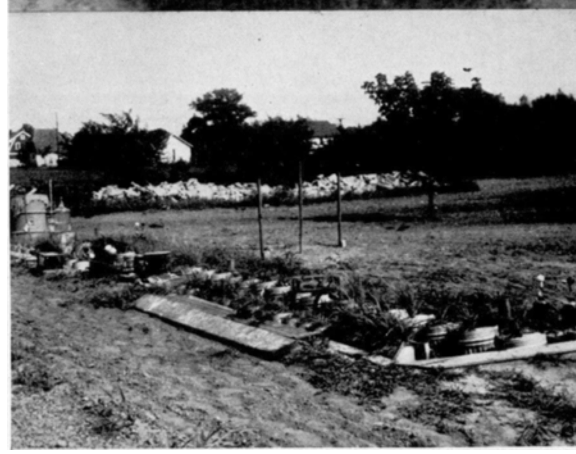


Fig. 2 (above). Representative grasses grown during 1937. Pot 85, *Agropyron Smithii;* pot 70, *Agropyron ciliare;* pot 81, *Bromus marginatus;* pot 30, *Agropyron ciliare;* pot 41, *Bouteloua gracilis.* The transpiration ratios for the last two potometers are not reported.

Fig. 3 (below). General view of the field site of the transpiration-ratio experiments conducted in 1937 and 1938.

the soil surface. All the potometers were placed in a compact row along the walls in such a manner that direct sunlight did not strike the sides of the cans.

Transpiration was determined daily except when atmospheric conditions were such that transpiration was small. The cans were weighed on small platform scales which had a capacity of 120 kg. and which were sensitive to 15 grams. The potometers were moved by hand to the scales. This was facilitated by mounting the scales on a rolling platform. Losses of water were replaced at the time of weighing with cistern water.

During the course of the experiment soil moisture in the potometers was maintained at 25 per cent of the dry weight of the soil. Since the moisture-holding capacity of the soil averaged 52 ± 2.6 per cent, this moisture content represented a near-optimum condition for plant growth and permitted free aeration of the soil.

The duration of the experiment was approximately 115 days. At the conclusion of this period the grasses were cut even with the soil surface, and the tops were dried to constant weight at 98° to 100°C.

Representative potometers for this series of experiments are shown in figure 2.

Experiments of 1938.—In general, the experimental procedures in 1938 were similar to those of the preceding year. The potometers were sealed and watered in the manner described for the experiments of 1937, and the species of grasses were the same for both years.

Most of the plants were grown in the greenhouse soil; however, it seemed desirable to grow some in a soil taken from the native habitat of these grasses. Fort Collins loam was selected for this purpose, and a shipment was obtained from Fort Collins, Colorado. This soil consists of a brown loam to a depth of about 10 inches. Below this is a chocolate brown compact silt loam approximately 9 inches deep. Plant roots are abundant in these two layers. The third layer, beginning at a depth of about 19 inches, is a dull brown silty clay loam flecked with white spots of lime. Very few roots penetrate into the third layer. This layer extends to a depth of about 33 inches. None of the subsoil below this level was used in these experiments. The A horizon of this soil may be considered as extending to a depth of 19 inches, and the B horizon from 19 to 33 inches. The two horizons were kept separate and at the time of potting were placed in their respective positions in the pots.

It has been shown repeatedly that the transpiration ratio is higher in an infertile soil than in a fertile one (Briggs and Shantz, 1913a, 1913b, 1914; Kiesselbach, 1916). Consequently, chemical analyses were made of the greenhouse soil and the Fort Collins loam in order to obtain an indication of the relative productivity of the two soils. The tests that were used give semi-quantitative information on the nutrient elements present in a dilute-acid extract of the soil (Spurway, 1938).

These tests indicated that nitrates, sulphates, ammonia, potassium, calcium, and magnesium were plentiful in both soils, the nitrates being especially abundant in Fort Collins loam. Phosphorus was low in the greenhouse soil, but moderate amounts were present in the loam. Aluminum, iron, and manganese were present in small but adequate quantities in both soils.

Two degrees of soil moisture were maintained in the experiments of 1938. These were chosen to represent intermediate and low levels, as indicated by the moisture-holding capacities and the wilting coefficients of the soils. Shantz (1925, 1927) has stressed the importance of using soil moistures determined by such soil constants, rather than moisture levels based only on abstract numerical relationship—i.e., percentages of 100, 80, 60, etc. The moisture-holding capacity was determined as the amount of water retained by the soil againt the force of gravity. The wilting coefficients were determined indirectly from the moisture equivalents of the soils, using the method of Briggs and Shantz (1912).[2] These authors define the moisture equivalent as the water-holding power of the soil against a force one thousand times gravity. The moisture equivalent divided by 1.84 gives the wilting coefficient of the soil.

The moisture-holding capacities of the A and B horizons of the Fort Collins loam, expressed as percentages of the dry weights of the soils, were 47.3 and 49.5, respectively; for the greenhouse soil the figure was 52.4 per cent. In the same order the moisture equivalents were 24.6, 28.0, and 29.8 per cent, and the wilting coefficients were 13.4, 15.2, and 16.2 per cent.

The degree of soil moisture chosen as representing intermediate conditions was 30 per cent of the dry weight of the soil for the greenhouse soil and 27 per cent for the loam soil. Each figure is slightly lower than the moisture level exactly midway between the wilting coefficient and the moisture-holding capacity of that particular soil. The low level of soil moisture, used only with the greenhouse soil, was 19 per cent of the dry weight of the soil. This figure is just slightly above the wilting coefficient for that soil.

Each of the three species of grasses was planted in six cans containing the greenhouse soil and in three cans containing Fort Collins loam. Of the six cans containing the greenhouse soil for each species, three were adjusted to the lower level of soil moisture, and the other three were brought to the higher level. All the cans containing Fort Collins loam were adjusted to the degree of soil moisture considered as being intermediate.

The method of admitting water to the pots was essentially the same as in the experiments of 1937. In all the pots which were to be maintained at the higher level of moisture, two of the watering devices were installed. For those potometers which were to be kept just above the wilting coefficient, three watering tubes were used. Shantz (1925, 1927) has shown that frequently a large part of the soil mass in potometers is never replenished with water and that in such experiments a considerable source of error is introduced. The admission of water through three tubes, and consequently at six well-separated points in the cans, was an effort to reduce this error.

The field site and the arrangement of the potometers for the experiments of 1938 was the same as that for the preceding year (fig. 3). Transpiration was measured every other day, and cistern water was added at the time of each weighing.

All plants grew satisfactorily (fig. 4–6) and were mature late in August when they were harvested. The tops were removed at the soil surface and dried to constant weight at 98° to 100°C. The roots were also harvested by washing them free of soil with a gentle stream of water. Their dry weights were determined in the same manner as the dry weights of the tops. The rhizomes of *Agropyron Smithii* were included with the roots of this grass.

Results and discussion.—The transpiration ratios of the three grasses for 1937 and 1938 are summarized in tables 1 and 2. These table show that *Agropyron ciliare* used the smallest amount of water

[2] Moisture-equivalent determinations were made by the Bureau of Chemistry and Soils, United States Department of Agriculture.

to produce a gram of dry tops under each condition, while *Agropyron Smithii* was consistently most extravagant in the use of water to produce tops. Although the differences between the transpiration ratios for the three grasses are not large, nevertheless they are substantial in most instances.

The transpiration ratios for the three grasses at 30 per cent soil moisture in 1938 were somewhat higher than the values obtained at 25 per cent soil moisture in 1937. This was probably due in part to the higher moisture level maintained during 1938; however, it would be expected that differences in climatic conditions prevailing during the two years would cause the transpiration ratio to vary.

Weekly evaporation from white and black spherical atmometers in 1937 averaged 202 cc. and 292 cc., respectively; in 1938 the figures, in the same order, were 184 cc. and 281 cc. The average relative humidity was 74.7 per cent in 1937 and 68.0 per cent in 1938. There were 8.33 inches of rainfall in 1937 and 7.34 inches in 1938. The daily average velocity of the wind was 2.1 miles per hour in 1937 and 1.9 miles per hour in 1938. In 1937 the mean daily air temperature was 21.4°C. The mean daily maximum and minimum temperatures were 27.5°C. and 15.8°C., respectively. In the same order the figures for 1938 were 20.9°C., 26.0°C., and 16.3°C. Light intensity, measured during the early afternoon of each day with a Macbeth illuminometer, averaged 9,028 foot candles in 1937 and 8,382 foot candles in 1938. All measurements of climatic conditions were made at the height of the experimental plants.

Several investigators have found that differences in the transpiration ratio correlate well with differences in evaporation (Briggs and Shantz, 1913b, 1914, 1917; Kiesselbach, 1916; Dillman, 1931). In these experiments the transpiration ratios were somewhat higher in 1938 than in 1937, but the weekly average evaporation from the white spheres decreased from 202 in 1937 to 184 in 1938. Evaporation from the black spheres, relative humidity, rainfall, wind velocity, temperature, and light intensity were also somewhat lower in 1938 than in 1937. With the exception of relative humidity, all climatic conditions favored higher transpiration in 1937; yet, the transpiration ratios were lower in 1937 than in 1938. The slightly higher moisture level in the second year appears to have caused the increase in the transpiration ratios.

Briggs and Shantz (1914) found the transpiration ratio for *Agropyron Smithii* to be $1{,}076 \pm 29$ at Akron, Colorado, in 1913. Dillman (1931) obtained the figures $1{,}247 \pm 31$ and 1,420 for this species at Newell, South Dakota, in 1913 and 1914, respectively. These values are much higher than the ones obtained in these experiments for this species. The explanation for the marked disagreement between the results of this investigation and those of the western investigations is found in the different meteorological conditions prevailing in the two regions. Evaporation and the average wind velocity are much higher in the northern Plains region than in southern Michigan. The mean daily temperatures

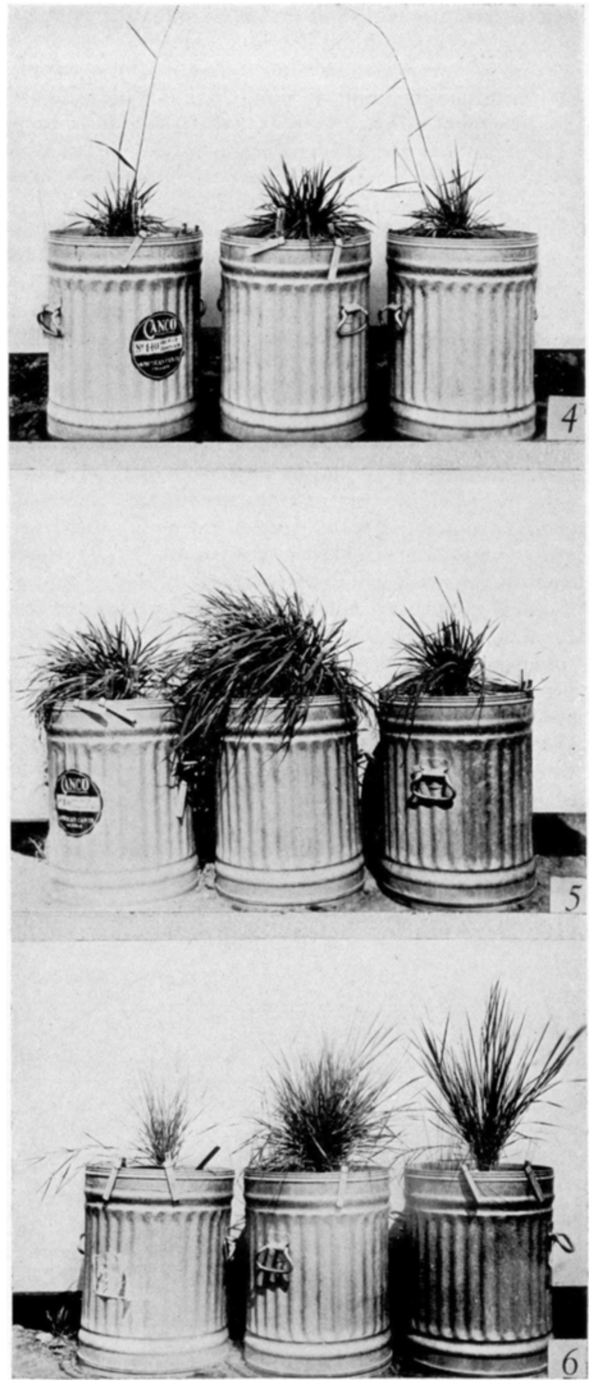


Fig. 4–6.—Fig. 4. *Agropyron ciliare* potometers grown in 1938. From left to right, greenhouse soil and 19 per cent soil moisture; greenhouse soil and 30 per cent soil moisture; Fort Collins loam and 27 per cent soil moisture.—Fig. 5. *Bromus marginatus* potometers grown in 1938. From left to right, greenhouse soil and 19 per cent soil moisture; greenhouse soil and 30 per cent soil moisture; Fort Collins loam and 27 per cent soil moisture.—Fig. 6. *Agropyron Smithii* potometers grown in 1938. From left to right, greenhouse soil and 19 per cent soil moisture; greenhouse soil and 30 per cent soil moisture; Fort Collins loam and 27 per cent soil moisture.

for the two areas do not differ significantly, but the average relative humidity is somewhat lower at Akron, Colorado, than that found in these experiments. Since the climatic conditions in Colorado and South Dakota favor high transpiration, it is to be expected that the transpiration ratios obtained in these localities would be higher than those reported here.

The transpiration ratio, by definition, is an expression relating transpiration to total growth increment; however, the practice of using only the dry weight of tops produced has been generally adopted as a basis for the expression. When forage production alone is being considered, this is a satisfactory procedure. In experiments in which no particular portion of the plant is being considered, such as forage, grain, roots, or tubers, it is desirable that the transpiration ratio should be based on total plant growth. Such an expression would also facilitate comparison of the transpiration ratios for these several types of crop plants. Sampson (1919) found that *Bromus marginatus* produced 17.6 per cent of its total growth as roots, as compared to 2.5 per cent for field peas and 3.2 per cent for wheat. A comparison of the transpiration ratios for these three plants gives misleading results, if only the tops are included in the calculation.

In the experiments of 1938 both roots and tops were harvested and kept separate during the process of drying. In the case of *Agropyron Smithii* the rhizomes were included with the root harvest. The proportions of the total dry matter produced as roots (and rhizomes) and tops are given in table 2.

The grasses used in this investigation produced a very large part of their total growth underground. In most instances the roots approached 50 per cent of the total growth. In the case of *Agropyron Smithii* the inclusion of rhizomes with the roots brought the percentage of subterranean growth to over 60 per cent. *Agropyron ciliare* produced a smaller part of its total growth as roots, the figures for this species being slightly less than 50 per cent.

When total plants were considered, in computing the transpiration ratios, *Agropyron Smithii* was most economical (table 2). On the basis of tops alone, this species was most extravagant. The high percentage of its total growth produced underground accounts for this difference. *Bromus marginatus* was least efficient in the use of water on the basis of total plants. The transpiration ratios based on total plants for the three grasses studied here are about half those values obtained with the tops alone in almost every instance.

It is not likely that the percentages of the total growth produced underground in these potometer experiments can be considered as a measure of those that would result under western field conditions; however, it seems probable that the roots of these grasses would comprise a significant proportion of their total growth in their native habitats. Unless a particular portion of the plant, such as forage or grain, is being considered, transpiration ratios for grasses should be based on total growth. This is especially true when plants are being evaluated for their usefulness for soil-conservation purposes in semiarid regions.

Two factors have been considered here which are important in evaluating plants with respect to their suitability for controlling soil erosion—viz., the proportion of their total growth produced under-

TABLE 1. *Transpiration ratios of grasses in 1937.*

Plant	Pot no.	Dry matter (tops) in grams	Transpiration in kg.	Transpiration ratio
Agropyron ciliare	68	25.8	7.1	274
	69	41.3	13.6	329
	70	34.0	13.3	391
	71	37.8	12.4	328
	72	36.7	14.5	394
	73	57.7	18.3	317
	Mean			339±17[a]
Bromus marginatus	75	31.2	15.6	499
	76	30.6	14.3	468
	77	25.9	9.4	365
	78	55.1	20.4	370
	79	32.4	14.0	431
	80	37.1	16.2	435
	Mean			428±19
Agropyron Smithii	66	36.6	13.3	364
	82	23.5	12.8	543
	83	24.2	11.2	464
	84	19.3	9.3	480
	85	25.7	12.6	488
	86	25.2	11.9	473
	Mean			469±21

[a] The standard error is given for all means.

ground and the ability to use water economically. Frequently it is recommended that grain crops should be used in soil-conservation projects; however, Sampson (1919) has pointed out that plants such as wheat have small root systems. From this standpoint, wheat is inefficient in stabilizing soil. On the other hand, the three grasses used in this investigation produced about one-half of their total growth underground. This high proportion of underground growth would indicate that these plants are superior to wheat with respect to their ability to bind soil.

It is true that most grasses are not so efficient as wheat and other small grain crops in the utilization of water (Briggs and Shantz, 1914; Dillman, 1931), even when roots are included in the determination of the transpiration ratio (Sampson, 1919). However, where stabilization of soil is of prime importance, the lack of efficiency in water utilization of the grasses is far outweighed by their marked superiority in the ability to bind soil.

The effect of the quantity of available soil moisture on the transpiration ratio is shown in table 2. These results are in agreement with those of previous investigators (Briggs and Shantz, 1913a; Kiesselbach, 1916). They show that all three grasses were considerably more economical at 19 per cent soil moisture than at 30 per cent. The relative transpiration ratios of the three grasses are essentially the same at the two moisture levels.

The transpiration ratios for the three grasses grown in Fort Collins loam are given in table 2. All

TABLE 2. *Transpiration ratios of grasses in 1938.*

Plant	Pot no.	Soil moisture in percent	Transpiration in kg.	Dry matter in grams: Roots[a]	Dry matter in grams: Tops	Transpiration ratio based on: Tops	Transpiration ratio based on: Total plants
			Greenhouse soil				
Bromus marginatus	60	19	15.7	46.7	36.0	437	190
	61	19	10.4	27.5	24.0	436	203
	62	19	18.7	41.7	45.1	415	216
	Mean					426±6	203±10[b]
	63	30	54.7	64.4	114.8	477	305
	64	30	45.0	35.8	90.9	494	355
	65	30	28.9	28.8	58.0	498	333
	Mean					490±5	331±11
Agropyron Smithii	66	19	6.3	28.5	14.2	443	148
	67	19	7.0	30.6	17.1	409	147
	68	19	7.8	28.0	18.0	435	170
	Mean					429±8	155±6
	69	30	31.9	119.6	60.4	528	177
	70	30	29.2	66.9	55.9	522	238
	71	30	34.4	103.8	67.5	510	201
	Mean					520±5	205±13
Agropyron ciliare	72	19	5.7	21.3	18.2	314	145
	73	19	4.6	16.4	12.3	372	159
	74	19	3.1	11.4	19.3	336	151
	Mean					350±14	152±4
	75	30	11.9	26.8	29.1	410	213
	76	30	12.9	29.7	30.1	429	216
	77	30	11.1	20.3	25.7	433	242
	Mean					424±6	224±7
			Fort Collins loam				
Bromus marginatus	78	27	8.4	10.4	11.3	744	388
	79	27	8.5	13.2	13.2	644	322
	80	27	8.9	11.9	11.3	787	384
	Mean					725±34	365±17
Agropyron Smithii	81	27	18.1	37.6	28.0	647	276
	82	27	15.2	38.4	19.2	791	264
	83	27	17.9	39.6	26.9	665	269
	Mean					701±36	270±3
Agropyron ciliare	84	27	9.5	11.8	19.6	485	303
	85	27	9.1	13.4	19.5	464	275
	86	27	8.4	13.8	15.1	554	289
	Mean					501±22	289±6

[a] Includes rhizomes of *Agropyron Smithii.*
[b] The standard error is given for all means.

three species required more water to produce a gram of dry material with Fort Collins loam than with the greenhouse soil.

In view of the chemical analyses of the two soils, these results were not in agreement with the results that were anticipated. Available nitrogen was more abundant in the native loam soil than in the greenhouse soil. No deficiencies in nutrients were detected in either soil. From the standpoint of nutrients the Fort Collins loam was probably better supplied than the artificial soil. On this basis it would be expected that the transpiration ratios would be lower with the native soil than with the artificial soil, since the transpiration ratio decreases with an increase in fertility of soils (Briggs and Shantz, 1913a; Kiesselbach, 1916).

A possible explanation of these unexpected results with Fort Collins loam is that 27 per cent soil moisture was not an optimum level for this soil. This moisture content is slightly lower than the moisture level exactly midway between the wilting coefficient and the moisture-holding capacity and was chosen to represent a favorable moisture level for growth. However, the plants growing in the loam soil at 27 per cent soil moisture did not do so well as did those growing in the greenhouse soil at 30 per cent soil moisture. It was not definitely ascertained that the soil moisture in the loam was too high for optimum growth; however, if this were true, the higher transpiration ratios with this soil would be expected, since the transpiration ratio increases with increasing soil moisture (Briggs and Shantz, 1913a; Kiesselbach, 1916).

SUMMARY

The transpiration ratio has been determined for three grasses suitable for use in soil conservation projects in the semiarid grasslands of the United States. The grasses used were *Agropyron Smithii*, *A. ciliare*, and *Bromus marginatus*. Plants were grown in large sealed metal cans, to which water was added frequently. The experiments were conducted under field conditions in an exposed site during 1937 and 1938.

The transpiration ratio—that is, the ratio between the amount of water transpired by the plant during its growth and the weight of dry matter produced—is expressed both on the basis of top growth and total plant growth. The figures based on total plants are about 50 per cent lower than those based on tops alone. Since roots (and rhizomes) comprised about one-half of the total growth of these grasses, their transpiration ratios should be based on total growth, at least when evaluating them for soil-conservation purposes in semiarid regions.

Agropyron Smithii was most efficient in the use of water when total plants were considered. On the basis of tops alone it was least efficient. *Agropyron ciliare* had the lowest transpiration ratio on the basis of tops produced but compared less favorably with the other two species when total plants were considered. *Bromus marginatus* used water inefficiently under all conditions. (See table 2.)

Although these grasses are less efficient in the use of water than grain crops such as wheat, their marked development of subterranean growth makes them superior plants for soil conservation.

The three grasses used water more economically at 19 per cent soil moisture than at 30 per cent soil moisture. The transpiration ratio for each species was materially altered by growing the plants in two different soils.

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